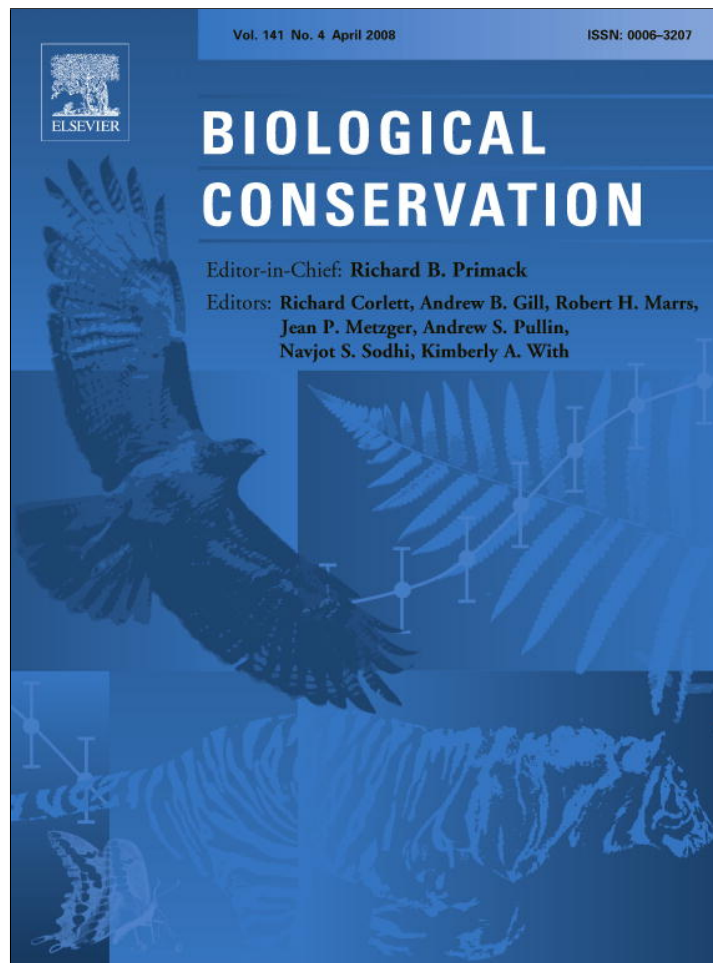


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Persistence of depleted abalones in marine reserves of central California

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ABSTRACT

We evaluated the persistence and possible recovery of two depleted marine mollusks, the red (*Haliotis rufescens*) and black abalone (*H. cracherodii*), in central California, USA. Monitoring over 32-years did not reveal increasing or decreasing trends in red abalone abundances and sizes over the past three decades, in the absence of harvesting. Comparisons between marine reserves protected for at least 25 years and sites with open public access showed significant difference in size structure for black abalone, with individuals greater than 8 cm in shell length comprising 14–37% of animals in reserves and 2–11% at open-access sites, and a trend for greater abundances of red abalone within reserves. Despite no increasing trends, protection in one of the no-take reserves, the Hopkins marine life refuge (HMLR), has led to persistence of red abalone populations over multiple generations, at average densities of 0.2 individuals/m². At other locations, both within the HMLR and elsewhere, red abalone densities are lower than at the location where long-term studies were conducted (av. 0.03 animals/m²), and an order of magnitude lower than for black abalone (av. 0.4 animals/m²). These results suggest that continued fishery closure and protection in no-take reserves are effective tools for allowing persistence of abalone populations, though there are no signs of recovery to levels comparable to those preceding fisheries collapse. Such failure to recover is most likely associated with high natural mortality and possibly continued illegal take, but not with processes underlying low abalone population levels elsewhere, including food or habitat limitation, recruitment failure, or disease. Linking current structure and trends to specific processes is a crucial first step towards devising focused strategies for conserving and re-building depleted marine populations.

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1. Introduction

A critical question that ecologists and conservation biologists attempt to answer is what processes allow populations to persist and recover after they have been reduced to low levels. In recent years, evidence of worldwide depletion of marine populations through overexploitation has accumulated (Myers and Worm, 2003; Kappel, 2005). It was long assumed that marine populations are able to recover once the main source of mortality (e.g., fishing) is removed. There is now evidence for low recovery rates following severe depletion in marine fish species with varying life histories (Hutchings, 2001; Hutchings and Reynolds, 2004). Processes that may slow or prevent recovery include: (1) failure to reduce fishing mortality (e.g., quotas set too high, illegal take, bycatch); (2) Allee effects (e.g., reduced reproductive success at low density; Allee, 1938); (3) habitat modification (e.g., loss and degradation of juvenile and/or adult habitat); (4) species interactions (e.g., alteration of competitive or predator-prey interactions); and (5) loss of genetic diversity and increased susceptibility to disturbance and disease. Thus, following the establishment of marine protected areas or fishery closures, empirical studies may reveal signs of recovery, including increased abundance, changes in size/age structure, and increased recruitment, whereas in other cases such evidence of recovery may be lacking, possibly due to one or more of the processes listed above.

California, USA, once supported fisheries for five species of abalone (*Haliotis* spp.). Precipitous declines in major abalone fisheries began in the late 1960s, with catches dropping from a peak of 24,000 tons to 115 tons by 1995, and culminating in the 1997 closure of all commercial and sport fishing south of San Francisco (Haaker et al., 1996; Rogers-Bennett et al., 2002). Intense fishing effort, El Niño events affecting feeding and reproduction, and disease all contributed to the declines (Tegner et al., 2000). Only a recreational fishery for red abalone (*H. rufescens*) still exists in Northern California (Haaker et al., 1996). White abalone, *H. sorenseni*, was the first marine invertebrate to be included in the US Endangered Species List in 2001, and black (*H. cracherodii*), green (*H. fulgens*), pink (*H. corrugata*), and pinto (*H. kamtschatkana*) abalone are now considered “species of concern”.

In response to conservation and economic concerns about the fate of abalone populations in California, the California Fish and Game Commission has recently released the Abalone recovery and management plan (ARMP, 2005), with the goals of reversing the decline of abalone populations that are in jeopardy of extinction, establishing self-sustaining populations throughout historic ranges, and reaching sustainable fishery levels in at least three-quarters of former ranges. Three criteria for assessing recovery of different populations were established: (1) broad size distribution (criterion 1), specifying that 25% of individuals should be larger than the legal size limit for each species; (2) densities above what estimated for minimum population viability (criterion 2), i.e., 0.2 individuals/m²; and (3) densities for fisheries sustainability greater than 0.66 individuals/m² (criterion 3).

Our goals were to evaluate the persistence and possible recovery of red (*Haliotis rufescens*) and black (*H. cracherodii*) abalone in central California, USA, and to examine alternative

hypotheses regarding processes that may promote or impede persistence or recovery of these populations. Factors and processes that may prevent recovery, or even underlie continued decline for some populations, include limited availability of resources, such as food and/or space (e.g., Tegner, 1989; Rogers-Bennett and Pearse, 2001), competitive or predator-prey interactions with other species (e.g., Hines and Pearse, 1982; Fanshawe et al., 2003), reproductive failure at low adult densities (e.g. Prince et al., 1988; Levitan et al., 1992; Tegner, 1993; but see Shepherd et al., 1992), disease (e.g., the withering syndrome; Raimondi et al., 2002), and continued fishing mortality through illegal take (Rogers-Bennett and Leaf, 2006). In particular, recent analyses of red abalone populations in California showed that in the presence of sea otters (*Enhydra lutris*), a major predator (Cox, 1962; Hines and Pearse, 1982; VanBlaricom and Estes, 1988; Estes et al., 2003; Fanshawe et al., 2003), abalones have lower densities, smaller sizes, and tend to be restricted to cryptic microhabitats (Fanshawe et al., 2003).

We used a variety of approaches to evaluate persistence or recovery of black and red abalone populations, and examine alternative explanations of what processes may underlie current patterns of abalone abundance and population structure. We examined long-term trends in the densities, population size structure, and mortality rates of red abalone over a 32-year period within the Hopkins marine life refuge, a no-take marine reserve protected since 1931, to examine temporal trends in populations in the absence of human take. We also used marine protected areas (MPAs) and *de facto* reserves, each protected for varying amounts of time (ranging 5–71 years) as a large-scale experiment for examining the consequences of past human disturbance on abalone's potential for persistence and recovery. We hypothesized that densities and sizes should increase with duration of protection of the sites. We asked whether habitat availability underlies variation in abalone abundance among sites by comparing habitat composition and refuge (rock crevice) availability across field locations, and we used our field data to examine evidence of abalone aggregation, which may play a role in increasing fertilization success. Finally, we tested the hypotheses that recruitment failures have occurred at low adult densities, and that variation in growth rates among sites, not mortality, underlies variation in size structure. To this end, we reconstructed age structure and growth rates of black and red abalone based on analyses of shell structure (e.g., growth rings) to examine the roles of recruitment and growth in influencing the trends observed across different sites. When combined, these approaches allowed us to ask: (1) is there evidence of recovery trends of black and red abalone populations of central California? (2) what are the habitat characteristics and demographic processes that may underlie observed patterns of variation in abundances and size structure of black and red abalone?

2. Methods

2.1. Long-term population trends in no-take reserves

Studies of red abalone population dynamics initiated within the Hopkins marine life refuge (HMLR) in 1972 by John Pearse

(University of California, Santa Cruz) and colleagues allowed us to examine long-term trends in red abalone densities, size structure, and mortality rates within a well-enforced no-take marine reserves, that is in the absence of human take. At the beginning of their study, a permanent 40 × 40 m plot encompassing granite outcrops interspersed with sandy channels and patches was established at 7–13 m depths (Hines and Pearse, 1982). Abalone surveys were conducted within the permanent plot between 1972–1981 (Lowry and Pearse, 1973; Cooper et al., 1977; Hines and Pearse, 1982), and subsequently repeated in 1990 (Pollard, 1992), and 1992 (Stoll and Bugbee, 1992). We repeated the surveys using identical methods in 2003–2004. No-take of all marine invertebrates was enforced throughout this entire time period.

Abalone abundances were quantified within 15–20 10-m² circular plots randomly placed within the 1600-m² permanent plot. All live abalones within the circular plots were identified to species, counted and measured to the nearest cm. Surveys were repeated five times, in January, April, and July 2003, and in August and October 2004. Mortality rates were estimated indirectly, following Hines and Pearse (1982), by quantifying accumulation rates of abalone shells within the permanent plot. The plot was delimited with plastic lines attached to cement blocks at each corner. The whole plot was searched systematically by multiple divers on six sampling dates between March and September 2003. All abalone shells found on the seafloor were removed. Shells were identified to species and measured to the nearest mm.

We assumed that colonization by macroscopic sessile invertebrates required weeks to months, and that unfouled shells had died recently. To test this assumption, we deployed 10 abalone shells with clean, shiny nacreous layers within a plastic crate in the HMLR permanent plot, subtidally, in July 2003 and checked the degree of fouling at monthly intervals over the following year. The inner nacreous layer of each shell was described as unfouled, lightly fouled (i.e., colonized by sessile invertebrates, including bryozoans, serpulid polychaetes, and vermetid gastropods), and heavily fouled. The first signs of colonization of the shells' nacreous layers by sessile invertebrates occurred after six weeks from deployment, and all shells were fouled after 11 months, confirming that unfouled shells represent mortality occurring within the past year.

2.2. Field surveys at sites protected for 5–71 years

We conducted field surveys at sites with varying current levels and past history of protection to examine possible trends and processes underlying persistence or recovery of abalones using spatial comparisons as a proxy for temporal change (e.g., Micheli et al., 2004; Russ et al., 2005). In particular we asked: (1) whether densities and size structure of black and red abalone differ between well-enforced no-take reserves and open-access sites; (2) whether densities and sizes of abalones increase with increasing length of protection at the sites; (3) if there is a relationship between spatial distribution of abalones (e.g., possible clustering) or habitat characteristics and availability of refuges and population densities at the sites.

Red abalones occur commonly from the low-intertidal zone to 20 m depths on rocky reefs, though they have been

reported at depths exceeding 60 m, whereas black abalones occur primarily in rocky-intertidal habitat (Cox, 1962), thus field surveys were conducted both subtidally and intertidally. Field surveys of abalone densities and population structure were conducted in September–November 2002 at eight intertidal and six subtidal sites distributed along a 35-km stretch of the central California coastline (Fig. 1) where restrictions of human access and collecting have been in place for variable lengths of time. In the HMLR (see above) and the point lobos ecological reserve (PLER), collecting of all marine invertebrates has been prohibited since 1931 and 1973, respectively (McArdle, 1997). Both no-take reserves are fenced and monitored by on site personnel and poaching has occurred infrequently since the reserves were established. At Pescadero Point and at a site just north of Mal Paso Creek, public access to the intertidal is restricted by private property. These sites can be accessed only through fenced estates. The presence of cliffs and channels prevents access from adjacent sites along the shore, although subtidal access is possible by boat. Thus, these rocky shores have been *de facto* intertidal reserves for at least 25 years at Pescadero Point (R. Spruance, Pebble Beach Co., personal communication) and at Mal Paso (K. DeNuccio, resident, personal communication), although poaching may occur subtidally at these sites. At Point Pinos, within the Pacific Grove Marine Gardens Fish Refuge, and Carmel Bay Ecological Reserve, collection of most mollusks and

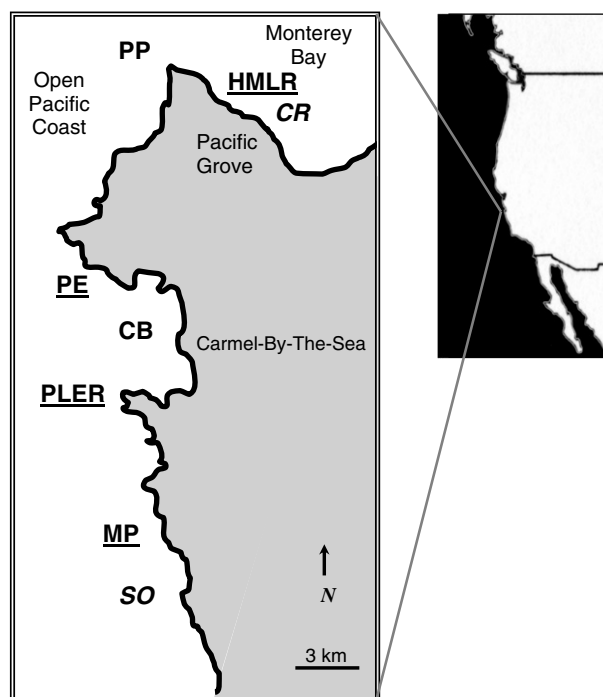


Fig. 1 – Map of the study area in central California showing the location of field sites: Cannery Row (CR, intertidal only), Hopkins marine life refuge (HMLR), Point Pinos (PP), Pescadero Point (PE), Carmel Bay (CB), Point Lobos ecological reserve (PLER), Mal Paso (MP), Soberanes Point (SO, intertidal only). Sites with restricted public access and effective enforcement of no-take regulations (no-take or *de facto* reserves) are underlined.

crustaceans was prohibited in 1984 and 1976, respectively (limited-take reserves; McArdle, 1997), although lack of continued surveillance makes strict enforcement of these restrictions impossible. At the remaining two sites, Soberanes Point and Cannery Row, collection of black abalones was allowed until 1993, while collection of red abalones was allowed until 1997, when all commercial and recreational abalone fisheries south of San Francisco were closed (Rogers-Bennett et al., 2002). Both sites lack continued surveillance and enforcement of harvesting regulations, and thus illegal take may occur.

At each site, abalones were identified to species, counted, and measured along seven-nine 30×2 m transects placed haphazardly, parallel to the shore at mid to high-intertidal elevations, and between 5 and 20 m water depth. Both in the intertidal and subtidal habitat, transects were located within rocky or boulder substrate though patches of sand interspersed among rocky outcrops were occasionally intersected.

Underwater flashlights were used to search for animals within rock crevices, both intertidally and subtidally. Maximum shell length was measured with calipers or rulers to the nearest cm. Along transects, we recorded the location of each animal (e.g., between boulders, in crevices, on exposed rock surfaces). Habitat quality was characterized by moving along the transect tape, recording the linear extent of different habitat types (e.g., sand; cobble, up to 30 cm diameter; boulders, between 30 cm and 2 m diameter; or continuous rocky substrate) underlying the tape. Widths and depths of rock crevices underlying the tape were measured to the nearest cm because abalones primarily occupy crevices in central California, and the size of available crevices has been hypothesized to be a critical factor influencing susceptibility to predators (Cox, 1962; Hines and Pearse, 1982).

Because of the low red abalone densities at most sites, and low black abalone densities at some of the sites (see Results), the number of individuals was too low to allow for statistical comparison of size-frequency distributions among all field sites. We augmented the subtidal surveys of red abalones in July and August 2004, and the intertidal surveys of black abalones in May 2005 with timed searches at four sites, the two no-take reserves with restricted public access and on site surveillance (HMLR and PLER), and the two limited-take reserves with open public access and no surveillance (Carmel Bay and Point Pinos) (Fig. 1). At each location, four investigators spent 80 min searching for black abalones intertidally, and 70–85 min for red abalones subtidally in multiple, non-overlapping sections of habitat. Each individual was measured to the nearest cm.

2.3. Age structure and growth rates

To determine whether missing age classes existed in local abalone populations, suggesting the occurrence of recruitment failure, we estimated the age of abalone shells collected in the HMLR, PLER, Point Pinos, and Carmel Bay Ecological Reserve. Abalone shells were aged by counting deposition rings, e.g., layers of calcite and aragonite deposited in the shells during growth, following the methods described in Shepherd et al. (2000). Red abalone shells with unfouled nacreous layers, i.e., recently dead, were collected between April and Sep-

tember 2003 within the permanent plot in the HMLR ($N = 119$ shells), and in August 2004 in the PLER ($N = 60$), Carmel Bay ($N = 25$), and Point Pinos ($N = 5$). Unfouled black abalone shells were collected between April and June 2005 along the HMLR shore ($N = 50$), the PLER ($N = 65$), Carmel Bay ($N = 44$), and Point Pinos ($N = 9$).

The spire of each shell was sanded using increasingly fine grits of sandpaper (240, 400, 600, 1500-grit) until a small hole appeared at the center of the spire. The sanded area was etched with diluted hydrochloric acid and growth rings were counted under a dissecting microscope. Rings were counted in four different directions for each shell, starting from the hole at the center of spires. Counts were then averaged to estimate the age of each shell. We tested the assumption that visible growth rings correspond to yearly growth increments by obtaining red abalones of known ages from a local aquaculture facility (the Monterey Abalone Farm Co., Monterey, CA). Shells of individuals 4.5, 5 and 6 years old ($N = 7$ shells, within each age group) were aged using the technique described above. The number of rings corresponded to the known age of individuals, averaging 4.76 (SE = 0.15), 5.19 (SE = 0.26) and 5.95 (SE = 0.20) for each age group, respectively. Despite some variation in counts among shells of identical age, the estimated ages were significantly different between the 4.5 and 5.0 and 6-year old shells (ANOVA: $F = 8.7$, $df = 2 \& 18$, $p = 0.002$, SNK tests at $\alpha = 0.05$), indicating that the aging technique could discriminate between different year classes.

In addition, we tested the accuracy of the aging technique by comparing growth ring patterns to annual fluctuations of stable oxygen isotope ratios (the ratio of ^{18}O to ^{16}O , $\delta^{18}\text{O}$) in the shell, which correspond to seasonal changes in ocean temperature (Gurney et al., 2004, and references therein). We conducted analyses of stable oxygen isotopes for one red abalone (11.9 cm in length, with 8 visible growth rings), and one black abalone (10.7 cm, 9 rings) shell. Shells were cleaned with diluted HCl to remove the periostracum, and were cut with a band saw along a curved transect perpendicular to the direction of growth. The prismatic layer was drill-sampled at approximately 1–2 mm intervals along the cut edge, taking care that the drill did not penetrate the inner nacreous layers of the shells. Between 60 and 100 μg of each sample was weighed and analyzed using a Finnigan MAT252 mass spectrometer coupled to a Kiel III carbonate device. The standard used was NBS-19 (SRM 8544), yielding a precision of better than 0.05‰ for $\delta^{18}\text{O}$. $\delta^{18}\text{O}$ values were converted to seawater temperatures using the paleotemperature equation for calcite reported in Gurney et al. (2004).

2.4. Statistical analyses

Abalone densities were compared among sites with varying restrictions of human use and access (Fig. 1) using nested ANOVA models with level of protection as the factor (with four levels for black abalone: no-take marine reserves, *de facto* reserves, limited-take reserves, and unprotected sites, and three levels for red abalone: no-take marine reserves, limited-take reserves, and unprotected sites), and site nested within human access (two sites for each level of the main factor). The assumption of homogeneity of variances was tested using Cochran's test (at $\alpha = 0.05$), and count data (No. individ-

uals/60-m² transect) were $\log(x + 1)$ -transformed when necessary. Separate analyses were performed for each species. The same ANOVA model was also used to compare the proportions of different types of substrate and the density of rock crevices at the field sites. Because % cover of substrate types were not independent, within each transects, we conducted separate analyses for each substrate type category. Abundances of black and red abalones from timed searches at the four sites were also analyzed using nested ANOVAs, with level of protection (limited-take vs. no-take reserves) as a fixed factor, and site (two sites for each level of protection) nested within level of protection. The timed searches conducted within each site were used as replicates ($N = 2$ sections searched for red abalones, $N = 4$ for black abalones). Spearman correlation was used to examine relationships between duration of protection, substrate characteristics, or refuge availability (i.e., crevices) and abalone densities mean size, and % of large individuals (i.e., above the legal size limit for each species) at the sites.

To test whether black and red abalones were distributed randomly or found in aggregations along transects for each site, we used methods from Underwood (1978) to calculate the expected number of quadrats (0.5×2 m) containing at least one abalone, for each transect. We calculated the mean deviation of the observed from expected number of quadrats containing at least one abalone among transects for each site and then tested for significant departures from zero using a t -test. Positive values indicate dispersed patterns while negative departures indicate clumped patterns.

We also used a second estimate of abalone clumping: the number of abalones found in a given crevice. We calculated the proportion of abalone individuals found in high quality crevices (defined as crevices with openings <10 cm wide, see "Results") binned into three abundance categories: (1) crevice with only one abalone; (2) crevices with two abalones; and (3) crevices with three or more abalones. To test whether the observed proportion of abalones in each class deviated from the pattern expected if abalone occurred in good quality crevices independently and with equal probability, we fit a Poisson distribution to the observed abundance data and tested whether this distribution described that observed for abalones in the field. We used our habitat surveys to estimate the proportion of crevices with <10 cm openings that had no abalone. Initial estimates indicated the proportion of unoccupied crevices ranged 71–93% intertidally, whereas 95% of crevices were estimated to be unoccupied subtidally (because of low abalone abundance all subtidal transects were pooled for analysis). To account for the uncertainty in the proportion of unoccupied crevices we fit a multiple Poisson distributions using the observed distribution of abalone abundance per crevice and a range of values for the unoccupied crevices. At each site we fit Poisson distributions assuming 70%, 80% and 95% of crevices were unoccupied, as well as using our empirical best estimate of abalone for each site derived from the habitat surveys. We used χ^2 tests to determine if the observed abalone per crevice distribution was described well by the best-fit Poisson distribution. Significant values indicate that a Poisson distribution poorly describes the distribution of abalone abundance per crevice. Due to low sample size, data from Cannery Row were excluded from this analysis.

Population size structure of black and red abalones was compared among sites and through time (at HMLR, only for red abalones) using Kolmogorov–Smirnov tests. To determine habitat preferences and assess the quality of different sites as abalone habitat, Kolmogorov–Smirnov tests were also used to compare the size distribution of available crevices with those occupied by abalones. Age frequency distributions reconstructed from shells were visually inspected to determine whether missing age cohorts were evident, suggesting that recruitment failure had occurred at the sites. An alternative explanation for the occurrence of missing age cohorts is the differential survivorship of different age classes, possibly resulting in low mortality and hence a lack of shells for specific ages.

Sizes and estimated ages of red and black abalones were fit initially to four growth functions: the Brody–Bertalanffy (Fabens, 1965; Ebert and Russell, 1992), Richards (1959), Jolicoeur (1985), Tanaka (1982) and Ebert et al. (1999) functions. All have been used before to model marine invertebrate growth (e.g., Ebert and Russell, 1992, 1993; Shelton et al., 2006). We fit each function to the data for each species using nonlinear regression (JMP 5.1 for Macintosh). Initial curve fitting showed when sites were fit separately parameter value confidence intervals overlapped, suggesting minimal differences between sites. For further analyses, all sites were pooled. To compare fits of the pooled data we used Akaike information criterion (AIC) weights to select the most parsimonious model for each species (Burnham and Anderson, 2002). Akaike weights (range 0–1) indicate the probability that the model is the best among the set of candidate models considered. For example, a model with an Akaike weight of 0.80 indicates that there is a 80% chance that it is the best model given the set of competing models.

All four functions fit the growth data well ($r^2 > 0.75$ in all cases). For both black and red abalones, the Richards function received the largest AIC weight (0.54 for black abalone, and 0.33 for red abalone) and for brevity will be considered exclusively for the remainder of this paper. The Richards function is

$$S_t = S_\infty(1 - be^{-Kt})^{-n}$$

where S_t is abalone length at age t , S_∞ defines the maximum shell length, K is the Brody growth parameter, and n is a shape parameter that allows for an inflection of S versus t ; S_∞ , K and n are fitted parameters. The parameter b was not fitted and was assumed to equal 1 because it is calculated as $(S_\infty - S_{\text{settlement}})/S_\infty$ and because the settlement size of abalone is very small (~ 0.1 cm), much less than S_∞ (Rogers-Bennett et al., 2003).

3. Results

3.1. Long-term population trends in a no-take reserve

Densities and size structure of red abalones within the HMLR permanent plot did not show increasing or decreasing trends over the past 32 years (Fig. 2). Densities have ranged 0.05–0.42/m² among sampling dates (1972–1981: 0.05–0.42/m², $\bar{x} = 0.19/m^2 \pm 0.02SE$; Lowry and Pearse, 1973; Cooper et al., 1977; Hines and Pearse, 1982; 2003–2004: 0.07–0.32/m²,

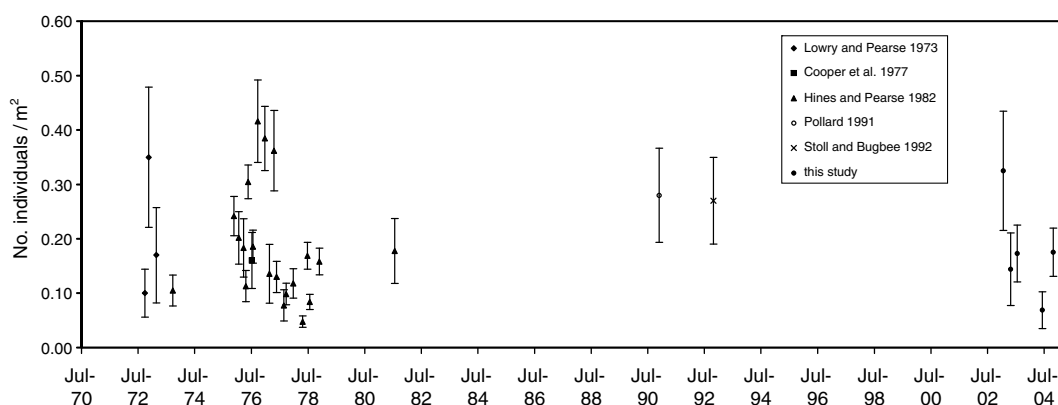


Fig. 2 – Temporal trends in red abalone densities within the 1600-m² HMLR permanent plot. Studies from which data were obtained are cited in the legend. Surveys were conducted, using identical methods, between 1972 and 2004 (N = 15–20 10-m² circular plots sampled on each date).

$\bar{x} = 0.18/m^2 \pm 0.04SE$; this study) and were not significantly different among years (1-way ANOVA: $F = 0.12$, $df = 2 \& 25$, NS). Thus, densities fluctuated around the threshold ($0.2/m^2$) estimated for persistence (criterion 2 in the Abalone recovery and management plan, ARMP, 2005) with no trend towards increased or decreased abundance over time and no density estimates approaching the threshold estimated for fishery sustainability ($0.66/m^2$; ARMP, 2005) (Fig. 2). Similarly, present size-frequency distribution (quantified in 2003–2004) does not differ significantly from those reported from other sampling periods (Kolmogorov–Smirnov tests: 1973 vs. 2003, $D = 0.12$, $N = 58,49$, NS; 1977 vs. 2003, $D = 0.12$, $N = 84,49$, NS; 1991 vs. 2003, $D = 0.13$, $N = 68,49$, NS). On different sampling dates, between 0% and 10% of individuals measured were larger than the legal size limit (17.8 cm), thus, criterion 1 in the ARMP (i.e., 25% of individuals larger than the legal size limit) was never met throughout the past three decades.

Rates of accumulation of unfouled (recently dead) abalone shells within the 1600-m² permanent plot have remained high throughout the last three decades (1972–1981: 29–87 shells/month, $\bar{x} = 49.7$ shells/month, $N = 9$ sampling dates, Hines and Pearse, 1982; 1992: 29 shells/month, $N = 1$ sampling date, Stoll and Bugbee, 1992; 2003: 20–49 shells/month, $\bar{x} = 34.6$ shells/month, $N = 6$ sampling dates, this study), suggesting high mortality rates throughout this time period.

3.2. Abalone abundances, size structure, and spatial distribution at sites protected 5–71 years

At intertidal sites, densities of black abalones (Fig. 3a) were highly variable among transects ($0–119/60\text{-m}^2$ transect, $\bar{x} = 0.36/m^2 \pm 0.06SE$). Mean black abalone densities were above the $0.2/m^2$ minimum viable population level at 5 of 8 sites, and above the $0.66/m^2$ threshold at one of the sites (Fig. 3a). There were no significant differences in black abalone densities with level of protection of sites either from belt transects ($F = 0.93$, $df = 3 \& 4$, NS), or from timed searches ($F = 0.6$, $df = 1 \& 2$, NS; Fig. 4b), and no relationship between local densities, mean size, and % of individuals larger than the legal size limit and duration of protection of each site (densi-

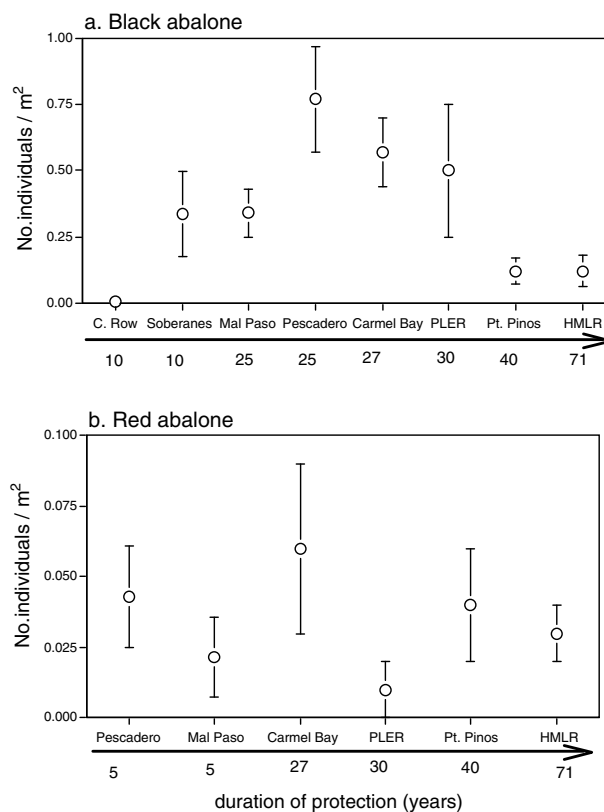


Fig. 3 – Densities of black (a) and red (b) abalones at intertidal (a) and subtidal (b) sites ranging from 5 to 71 years of protection from collecting and fishing. Average ($\pm 1 SE$) densities (No. individuals/m²) from seven $30 \times 2\text{-m}$ transects surveyed at each site are reported.

ties: $R = 0.21$, $N = 7$, NS; mean size: $R = -0.02$, $N = 7$, NS; % large individuals: $R = 0.26$, $N = 7$, NS). Size-frequency distributions of black abalones were significantly different between the four open-access and four restricted-access sites where belt transect surveys were conducted ($D = 0.21$, $N = 435,724$, $p < 0.001$; size-frequency distribution not shown). Black abalones larger than the legal size limit used in the

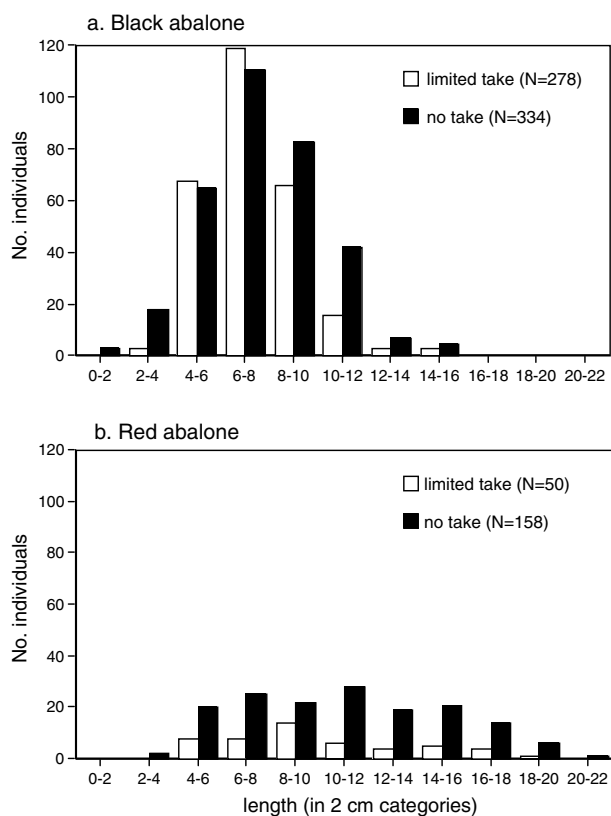


Fig. 4 – Size-frequency distribution of black (a) and red (b) abalone within no-take (i.e., restricted-access sites, HMLR and PLER), and limited-take reserves (i.e., sites with open public access, Point Pinos and Carmel Bay). The total number of individuals measured during timed searches conducted at each site (see “Methods”) is reported in parentheses.

recreational fishery conducted until 1993 (12.7 cm) were found almost exclusively within no-take or *de facto* reserves (between 0.6% and 6% of total individuals, at different sites), where they never accounted for 25% of total individuals (criterion 1 in the ARMP, 2005). At a size of 8 cm in length, black abalones appeared to become more abundant in no-take or *de facto* reserves (14–37% of individuals larger than 8 cm) compared to open-access sites (2–11%). Timed searches confirmed results from the belt transect surveys of black abalones (Fig. 4a). Size-frequency distributions of black abalones were significantly different between well-enforced no-take reserves and sites with open public access ($D = 0.12$, $N = 334,236$, $p < 0.05$; Fig. 4a). No-take reserves had both more small (<4 cm) and large (>8 cm) individuals than open-access sites (Fig. 4a).

Densities of red abalones at subtidal sites were an order of magnitude lower than densities of black abalones at intertidal sites (between 0 and 10/60- m^2 transect, $\bar{x} = 0.03/m^2 + 0.007SE$, Fig. 3b) and not significantly different across levels of protection ($F = 3.1$, $df\ 2\&\ 3$, NS) when densities were quantified with belt transects. Thus, although at some locations densities can be higher (e.g., in the permanent plot within the HMLR, where densities have averaged 0.2/ m^2 over the past three decades, see *Long-term population trends in a no-take reserve*), red abalone

densities were considerably lower than the 0.2/ m^2 threshold (criterion 2; ARMP) at a majority of the sites we examined, with the exception of the permanent plot.

In timed searches, red abalones tended to be more abundant in no-take reserves than in limited-take, open-access sites, though the p -value was close to but not lower than the 0.05 significance level ($F = 14.2$, $df\ 1\&\ 2$, $p = 0.06$; Fig. 4b). As for black abalone, there was no relationship between local densities, mean size, or % large individuals of red abalones and duration of protection of sites (densities: $R = 0.04$, $N = 6$, NS; mean size: $R = 0.50$, $N = 6$, NS; % large: $R = 0.12$, $N = 6$, NS). Individuals larger than the legal size limit for red abalone (17.8 mm in shell length) accounted for 0–2.6% of total individuals measured at sites with open public access, and between 4.2% and 5.7% in well-enforced reserves, in all cases well below the 25% level under criterion 1 of the ARMP. Size-frequency distributions of red abalones, quantified through timed searches, were similar between no-take reserves and limited-take, open-access sites ($D = 0.166$, $N = 159,50$, NS; Fig. 4b). Densities of red abalones in belt transects were too low to evaluate among site differences in size structure.

Analysis of patterns of spatial dispersion of black abalones along transects shows significant clustering at all sites (d values ranging -9.9 to -17.3 ± 3.1 to 4.3 SE, $df = 6$, $p < 0.05$) except Point Pinos ($d = -4.9 \pm 2.4$ SE, $df = 4$, NS) and HMLR ($d = -5.1 \pm 2.7$ SE, $df = 4$, NS). The non-significant clustering in these two sites may be due to the low densities of black abalones (Fig. 3a). Dispersion of red abalones was not significantly different from random at any site (d values ranging -0.5 to -2.3 ± 0.3 to 1.4 SE, $df = 2$ to 5 , NS). However, this is likely due to low densities of red abalones at all sites (Fig. 3b). A majority of the 30×2 m transects (76%) harbored four or fewer red abalones. When red abalones were found in densities greater than four animals/transect, significant clumping did occur ($d = -8.7 \pm 0.5SE$, $df = 5$, $p < 0.01$).

Similarly, the distribution of abalones per crevice <10 cm in width deviated from the expected Poisson distribution at all sites and for all scenarios including different estimates of unoccupied crevices (χ^2 tests: $p < 0.0001$ at all sites), indicating that abalones were not distributed randomly between good quality crevices. For all sites, there was a disproportionate abundance of crevices with three or more abalones (Table 1). Abalones who were found alone during surveys made up 5–24% of individuals intertidally and 33% of individuals subtidally, indicating that a majority of individuals were in close proximity to another abalone.

3.3. Abalone habitat use and variation in habitat characteristics among sites

All red abalones and a majority (97%) of black abalones encountered in surveys occupied crevices in rocky outcrops or between large boulders. Both species tended to occupy crevices narrower than 10 cm wide with greater frequencies than expected based on availability of different sized-crevices at the sites (black abalone: $D = 0.39$, $N = 290,321$, $p < 0.001$; red abalone: $D = 0.48$, $N = 223, 52$, $p < 0.001$, Fig. 5).

Comparisons of habitat characteristics among levels of access and protection of sites showed that there were no significant differences in substrate composition both

Table 1 – Total proportion of abalones found in three abalone-per crevice classes

Site	1	2	3+
<i>Intertidal</i>			
Carmel	0.05	0.08	0.87
HMLR	0.23	0.21	0.56
PLER	0.11	0.03	0.86
Mal Paso	0.24	0.12	0.64
Pescadero	0.11	0.11	0.79
Point Pinos	0.22	0.16	0.62
Soberanes	0.04	0.15	0.81
<i>Subtidal</i>			
All Sites Pooled	0.33	0.22	0.45

Abalone were classified as being alone (class “1”), with a single other abalone (class “2”), or with two or more other abalone (class “3+”) within a given crevice.

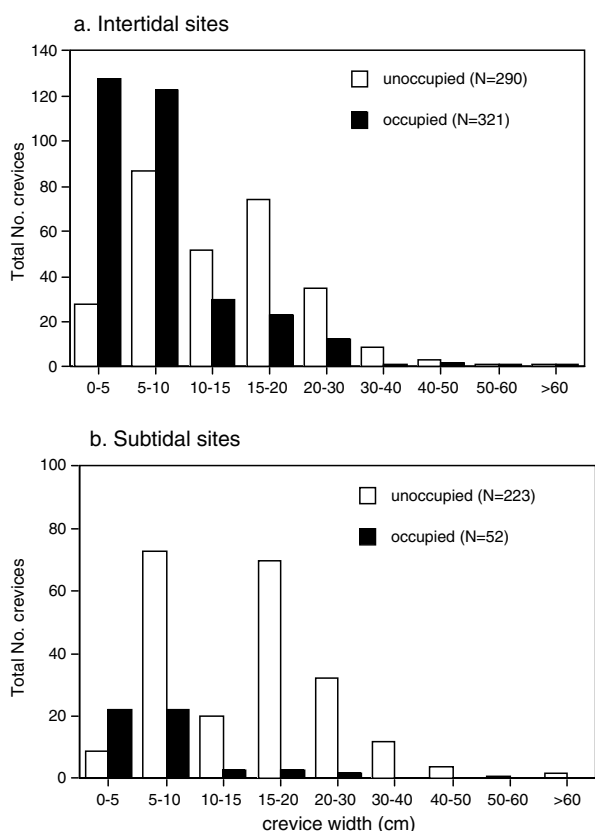


Fig. 5 – Size-frequency distribution of crevices of varying widths at intertidal (a) and subtidal (b) sites. Numbers of unoccupied crevices and numbers of crevices occupied by black (a) and red (b) abalone, pooled across all sites, are reported separately for each size bin. Total numbers of occupied and unoccupied crevices surveyed are reported in parentheses.

intertidally and subtidally (ANOVA: NS for all variables; Table 2). In particular, there was no difference in the availability of preferred habitat (crevices narrower than 10 cm; Table 2). There were no significant correlations between any of the

variables describing habitat characteristics of sites and the densities of black ($R = 0.19$ – 0.36 , $N = 56$, NS) or red ($R = 0.03$ – 0.20 , $N = 42$, NS) abalones along transects.

3.4. Possible recruitment failure: indirect evaluation from age structure of recently dead shells

To determine whether recruitment failure has occurred in recent years at our field sites, we reconstructed the age structure of recently dead red and black abalone. Recruitment failure would result in missing age classes, whereas a representation of individuals in all age classes would suggest that abalones have recruited successfully every year. The age of recently dead abalone shells collected at the HMLR, PLER, Carmel Bay, and Point Pinos, estimated based on shell growth rings, ranged between 1 and 14 years for red abalones, and 2 and 19 years for black abalones (Figs. 6 and 8). In no-take reserves (HMLR and PLER), all age cohorts within the past ten years were represented, suggesting that red and black abalones had recruited successfully every year over at least a decade (Fig. 6). Within Carmel Bay, no black abalone shells 1–3 years old were retrieved (Fig. 6a). Only 25 red abalone shells in total were found in Carmel Bay, and even fewer for both species at Point Pinos (data not included in comparisons of age structure among locations due to few shells).

In addition to validating our ageing technique using red abalones of known ages from a local aquaculture facility (see “Methods”), we compared shell growth rings with seasonal variation in seawater temperatures, reconstructed using isotope analysis. The black abalone shell, with nine calcite rings at the spire, showed possibly seven-eight seasonal peaks in seawater temperatures estimated from $\delta^{18}\text{O}$ (Fig. 7a). The red abalone shell, with eight growth rings, showed possibly eight peaks (Fig. 7b). Although peaks are more evident for the red than black abalone shell, in both cases high overall variability makes it difficult to discern seasonal peaks. Thus, further analyses are needed to confirm that ring deposition occurs on a yearly basis, though growth ring patterns in shells of known ages from aquaculture facilities support this hypothesis for red abalone (see “Methods – Age structure and growth rates”).

3.5. Reconstruction of shell growth rates

Curve fitting of age and size data from recently dead shells, conducted separately for each site, yielded growth parameter estimates with overlapping confidence intervals, suggesting no significant differences in growth rates exist among the sites (Fig. 8). Individual growth parameters obtained by fitting the Richards growth equation to the pooled data for each species were 12.4 cm (95%CI: [11.3, 14.0]) for S_{∞} , 0.26 [0.18, 0.33] for K , and -2.37 [$-3.39, -1.70$] for n for black abalones, and 15.8 cm [13.8, 20.5] for S_{∞} , 0.16 [0.08, 0.23] for K , and -1.21 [$-1.57, -0.93$] for n among red abalones.

4. Discussion

Our results suggest that recovery of abalone populations in central California is limited by high rates of mortality, as

Table 2 – Comparisons of habitat characteristics among the field sites

Habitat type	C. Row	HMLR	Point Pinos	Pescadero	C. Bay	PLER	Mal Paso	Soberanes
<i>a. Intertidal sites</i>								
Rocky outcrop	63.2 (10.6)	65.5 (3.1)	52.8 (6.1)	69.4 (6.0)	65.0 (8.2)	90.0 (3.8)	84.7 (2.5)	87.9 (3.9)
Boulders	23.6 (8.7)	9.4 (4.4)	34.2 (5.3)	10.8 (6.0)	24.7 (9.9)	2.3 (2.3)	3.4 (1.9)	3.6 (3.6)
Cobble	0	0	1.8 (1.8)	1.4 (0.9)	0	0.6 (0.6)	0	0
Sand	0	0	0	0	0.4 (0.3)	0	0	0.8 (0.5)
No. crevices	3.8 (1.1)	8.0 (1.3)	6.0 (1.6)	11.7 (1.7)	4.3 (1.2)	4.0 (1.3)	3.8 (0.9)	3.1 (0.6)
No. cr. <10 cm	1.4 (0.5)	2.0 (0.8)	3.0 (0.7)	3.7 (0.8)	2.4 (0.7)	1.1 (0.5)	1.4 (0.5)	1.6 (0.7)
		HMLR	Point Pinos	Pescadero	C. Bay	PLER	Mal Paso	
<i>b. Subtidal sites</i>								
Rocky outcrop		50.8 (8.9)	33.9 (6.8)	69.5 (9.9)	62.0 (5.5)	93.9 (4.1)	77.7 (8.5)	
Boulders		31.2 (8.1)	50.4 (7.0)	26.9 (9.4)	30.0 (6.2)	1.8 (1.8)	17.2 (8.3)	
Cobble		0	1.4 (1.4)	0	0	0	1.0 (1.0)	
Sand		12.5 (3.3)	10.4 (3.8)	0.2 (0.2)	0.5 (0.5)	0	0	
No. crevices		4.7 (0.8)	2.0 (0.8)	5.5 (0.8)	9.6 (2.2)	5.6 (2.7)	4.0 (0.8)	
No. cr. <10 cm		1.3 (0.3)	1.3 (0.7)	2.4 (0.5)	3.0 (0.9)	2.0 (0.8)	1.8 (0.6)	

Mean percent cover (± 1 SE in parentheses) of rocky outcrops, boulders, cobble, and sandy bottom, mean number of crevices, and mean number of crevices narrower than 10 cm wide along seven 30-m linear transects surveyed at each site are reported. No significant differences among different access levels for the sites were found in nested ANOVAs (see “Methods”).

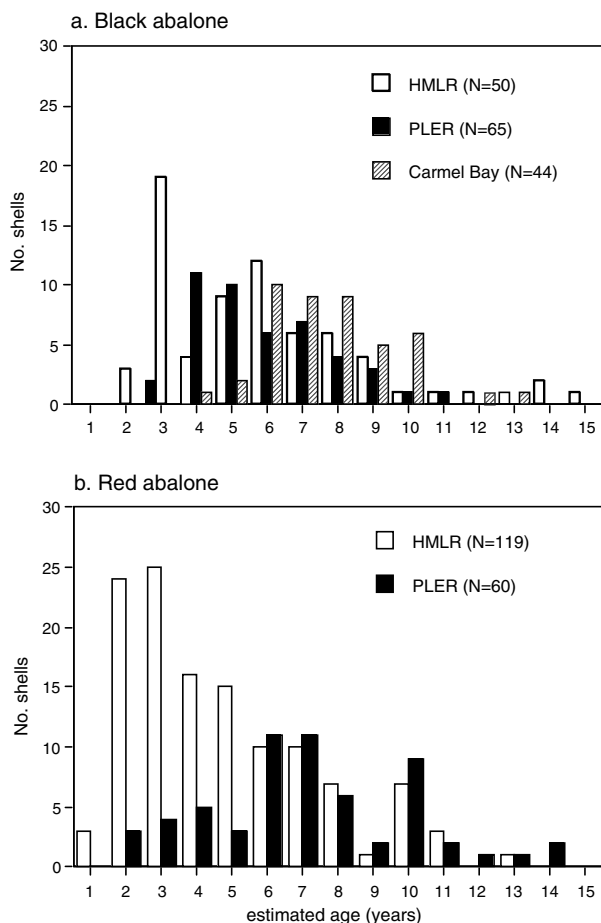


Fig. 6 – Age structure of recently dead black (a) and red (b) abalone. The total number of shells aged for each site is reported in parentheses. Data from Carmel Bay (for red abalone) and Point Pinos (both species) are not reported because few shells (between 5 and 25) were retrieved at these sites.

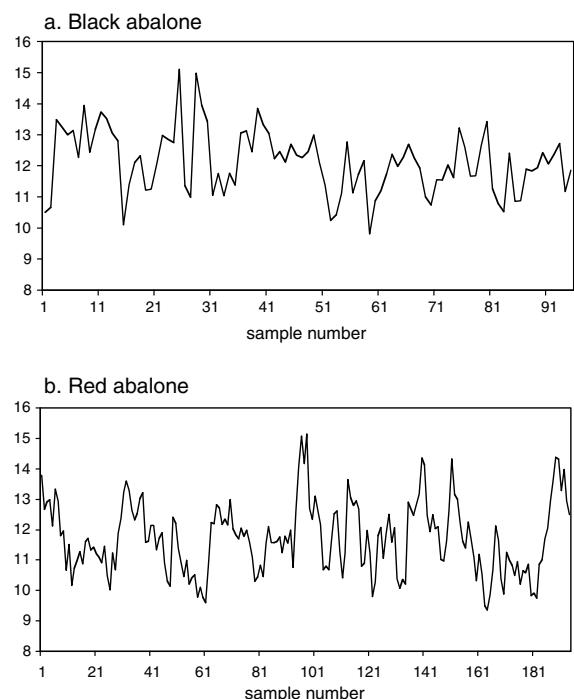


Fig. 7 – Sea water temperature (°C) estimated from $\delta^{18}\text{O}$ of one black (a) and one red (b) abalone shell. $\delta^{18}\text{O}$ were quantified from samples collected at 1–2 mm intervals along a curved transect perpendicular to the direction of growth of each shell (see “Methods”). The black abalone shell had nine visible growth rings at the spire, the red abalone shell had eight rings.

suggested by the high rates of production of shells, and possibly ongoing illegal take but not by habitat or food limitation, or recruitment failure. Our results also suggest that abalone populations can persist at the current

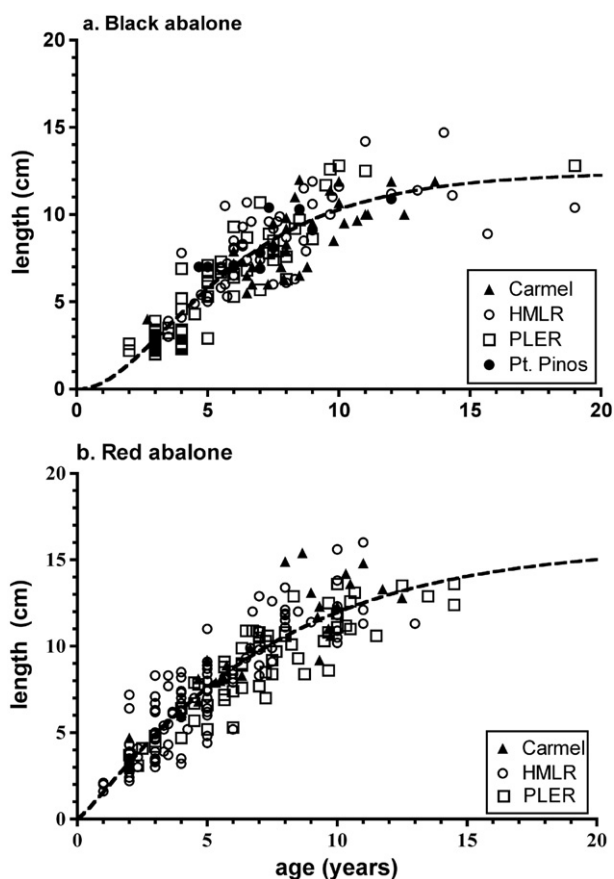


Fig. 8 – Size-age relationships for black (a) and red (b) abalone shells collected at the two no-take (HMLR and PLER) and limited-take (Point Pinos and Carmel Bay) reserves. Richards curves, fitted after pooling data among sites, are shown.

low densities, though recovery to levels that can support fisheries has not occurred in the presence of sea otters.

Abundances of red abalones at sites in central California are substantially lower than historical levels and targets set for recovery (*Abalone Recovery and Management Plan*, 2005), even within well-enforced areas protected from human take of abalones for over 30 years. Mean densities and proportions of large individuals did not increase during the past three decades within a no-take reserve (the HMLR; Fig. 2) or at sites protected for at least two decades (Fig. 3). At all sites, except for the permanent plot within the HMLR, average red abalone densities are well below the threshold established for Minimum Viable Populations of 0.2 individuals/m² (criterion 2, ARMP). Within the permanent plot of the HMLR, densities have averaged 0.2 individuals/m² for the past 30 years (Fig. 2), consistent with the expectation that these densities allow for successful recruitment of abalones. Black abalone densities at sites outside Monterey Bay have densities above this threshold, and even above the 0.66 individuals/m² threshold set for populations that can sustain fisheries (criterion 3) at one site (Fig. 3). However, at no sites are 25% of individuals above the legal size limit of 12.7 cm and 17.8 cm for black and red abalone,

respectively (criterion 1). Given that even at sites protected from human take for several decades the percent of individuals larger than the legal size limit was 10% at the most (within the permanent plot of the HMLR) and more commonly less than 6% at the other locations within reserves that we surveyed, the threshold set under criterion 1 may not be met for central California populations within the sea otter's range.

The lack of either increasing or decreasing trends in abalone densities and size structure, both examined from the long-term trends within the HMLR and across multiple sites with varying durations of protection, indicates that under current conditions local abalone populations show no signs of recovery to levels attained during the 1950–60s, before fisheries collapses (that occurred in the 1970–80s, depending on the species and region; *Rogers-Bennett et al.*, 2002) and sea otter recovery (sea otter re-colonized central California in the late 1950s–early 1960s, *Hines and Pearse*, 1982). Because abalone fisheries exploitation predominantly occurred while sea otter populations were extremely depressed, a baseline for abalone populations in the presence of sea otters is not available. The current levels of abalone populations in central California may reflect conditions prior to both fishing and the near-elimination of sea otters from this region, characterized by intense otter predation and low but stable densities of abalones.

Unfortunately, quantitative information on abalone densities and size structure at our sites for the 1950–60s (before otter recovery) is not available, though anecdotal information and data from other regions suggest abundances were much greater than at present. Within the HMLR in the late 1950s, prior to sea otter re-establishment in Monterey Bay, *McLean* (1962) reported that abalone and sea urchins were very abundant, and “spaced only a few feet apart”. At northern California sites, outside of the current range of sea otters, red abalone densities range 0.6–0.9/m² (*Fanshawe et al.*, 2003). *Richards and Davis* (1993) reported black abalone densities between 27 and 74 individuals/m² in the Channel Islands, in the absence of sea otters and before mass mortality from the withering syndrome.

At our sites, rates of natural mortality in the absence of human take have remained high over the past three decades. The rates of production of recently dead abalone shells in the HMLR, an indirect measure of abalone mortality rates (*Hines and Pearse*, 1982) are similar between time periods immediately following re-establishment of sea otters in Monterey Bay, in the 1990s, and in recent years (2003–2004). Stable abundances and size structure of red abalones despite high mortality rates are possibly due to a combination of consistent recruitment (Fig. 6) and the presence of refuges from predators (e.g., deep, narrow crevices, within which all live abalones were found). The abundance of deeply creviced rocky outcrops within the permanent plot of the HMLR (*Hines and Pearse*, 1982) may explain the locally greater densities documented within the plot (av. 0.2 individuals/m²) relative to the other sites surveyed (av. 0.03 individuals/m²), which encompass a broader range of habitat characteristics.

Red abalone showed a trend for greater abundances within no-take, well-enforced reserves compared to lim-

ited-take reserves with no on site surveillance (Fig. 4). For black abalone, we found significantly greater proportions of large animals in the absence of human take – in well-enforced no-take reserves and in *de facto* reserves with no public access to the shore. In fact, black abalones larger than the legal size limit were almost exclusively observed within reserves. Increased abundance and proportions of large individuals is one of the most commonly documented effects of marine reserves on a suite of species (e.g., Halpern, 2003), including abalones (Edgar and Barrett, 1999; Wallace, 1999). This observed response of population structure to protection is important because the fecundity of many fishes and invertebrates increases disproportionately with size, and therefore enhanced abundance of larger, older individuals may result in greater reproductive output from populations protected in reserves (Bohnsack, 1998; Paddock and Estes, 2000). Since sufficient time has elapsed since the implementation of bans on legal fishing to eliminate differences in size structure between no-take reserves and other areas (Fig. 8), this difference in size structure between no-take and limited-take sites may suggest that some poaching of larger individuals persists outside reserves despite the fishing ban. However, data on poaching are lacking and a direct evaluation of this hypothesis is impossible.

There is no evidence that habitat quality and availability explains variation in abalone abundances and size structure among sites, or that limits overall recovery of these populations. Unoccupied crevices of suitable size were available at comparable densities at all sites (Table 2 and Fig. 5). Similarly, we have no evidence of disease affecting these populations. During our many hours of observation, we never encountered diseased abalones. Sea otters, the main predators of abalone in this area, were observed at all sites (unpublished sea otter monitoring data, USGS-BRD-Western Ecological Research Center, Santa Cruz, CA, and personal observations), but inter-individual variation in feeding preferences strongly determines the impacts that otters may have on abalones at different sites (Estes et al., 2003). Other potential predators observed at the sites, including the sea stars *Pycnopodia helianthoides* and *Pisaster giganteus*, crabs *Cancer* spp., fishes, and octopus could also vary in their abundances and predation impacts on abalone. Indirect effects of protection in marine reserves through modification of species interactions have been documented in several instances (e.g., Pinnegar et al., 2000; Baskett et al., 2007), offering a possible alternative explanation to direct impacts of human take for the variation observed between reserves and unprotected areas. Although we cannot evaluate this hypothesis because of lack of quantification of predation rates at the sites, this explanation seems unlikely because protection of predators in no-take reserves would likely increase, not decrease predation mortality of abalone and other invertebrates.

Greater growth rates at the sites with well-enforced restrictions of public access and take would also lead to an accumulation of large individuals in the population. However, this alternative mechanism is not supported by our data. Growth curves we reconstructed for a subset of the sites are completely overlapping among the sites,

including both reserves and open-access sites, suggesting that growth rates are similar across the sites (Fig. 8). In addition, growth rates estimated at our field sites are within the range reported for black (Blecha et al., 1992; Haaker et al., 1995) and red abalone (Tegner, 1989; Haaker et al., 1998) elsewhere, indicating that resource availability is not likely to be limiting abalone recovery in this area.

As with other invertebrates, low densities are of great concern for successful reproduction in abalone populations (Levitan et al., 1992; Babcock and Keesing, 1999). Despite low local abalone densities, we found no evidence of declining abundances (Fig. 2) or of missing age cohorts (Fig. 6). In the no-take marine reserves, high abundances of juveniles and representation by individuals in all age classes over the past decades suggest abalones are recruiting successfully every year. The indirect reconstruction of age structure from recently dead shells cannot be used to quantify year-to-year or site-to-site recruitment variation because it is confounded by possible temporal and spatial variation in processes influencing shell production. However, the lack of missing age cohorts over the past decade does suggest that recruitment failures have not occurred at these sites. The tendency of abalones to aggregate likely alleviates problems related to fertilization. Thus, the presence of aggregations of adult abalones may be crucial for maintaining abalone recruitment at low current densities. Estimates based on the distribution of the number of abalones per crevice suggest that a majority of individuals are in close proximity to other individuals (Table 1).

Taken together, these results highlight the variety and complexity of factors and interactions underlying the dynamics of marine populations and their responses to natural disturbance and management interventions. A radical intervention, such as the closure of a fishery, occurs in the context of other simultaneously changing conditions. Thus, predicting and evaluating the consequences of a management action requires an understanding of the demographic and ecological processes controlling populations, and of the longer-term historical context in which variation in natural and human disturbances affecting the ecosystem have occurred. In the specific case of central California abalones, persistence at low densities within well-enforced marine reserves suggests that high predation pressure is compensated by continued recruitment and by the availability of habitat containing natural refuges, i.e., deeply creviced rocky outcrops offering refuges from predation. Persistence over larger scales, outside well-enforced but generally small marine reserves, may require continued and improved regulation of human take, e.g., by minimizing mortality of abalones through education programs and renewed enforcement (Rogers-Bennett and Leaf, 2006). Re-building depleted local abalone populations, particularly to levels that may support fisheries may require additional, active interventions, such as outplanting abalones in aggregations within habitat containing natural refuges (e.g., crevices that are inaccessible to sea otters). More generally, linking current structure and trends to specific processes is a crucial first step towards devising focused strategies for conserving and re-building depleted marine populations.

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